






Research Article

Interaction intensity as determinant of geographic range overlap between ant-following birds and army ants

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Abstract

Biogeography has as a central theme, which is the study of geographic ranges of species that are determined by evolutionary history, abiotic factors, and biotic interactions. Understanding the influence of biotic interactions on geographic ranges is a topic that has been little explored, especially in a way that compares species that vary in intensity of interaction. Here, we assessed interaction intensity as a determinant of geographic range overlap between ant-following birds and army ants in Mexico and Central America. We hypothesized that the intensity of the interaction between army ants and ant-following birds, obligate or facultative, predicts the overlap of geographic ranges of interacting species, as well as the extension of geographic ranges. We generated species distribution models with MAXENT and estimated the percentage of overlap between two species of army ants and 10 species of ant-following birds. Contrary to our predictions, Bayesian regression models found no support for an estimated higher range overlap for obligate ant-following birds and army ants, or wider geographic ranges for facultative ant-following bird species. However, our results suggested trends for higher percentages of range overlap between obligate ant-following birds and army ants, and for geographic ranges of facultative ant-following birds extending to areas without the presence of army ants. Our research encourages further exploration of the biogeography of biotic interactions as part of a quantitative gradient of intensities and not as qualitative categories, integrating spatial and temporal variation in the intensity of interaction.

Resumen

La biogeografía tiene como tema central el estudio de las áreas de distribución, las cuales están determinadas por la historia evolutiva, los factores abióticos y las interacciones bióticas. Comprender la influencia de las interacciones bióticas en las áreas de distribución es un tema que ha sido poco explorado, especialmente en la comparación de especies que varían en intensidades de interacción. En este estudio evaluamos la intensidad de la interacción como determinante del traslape entre las áreas de distribución de aves seguidoras de hormigas y hormigas soldado en México y América Central. Hipotetizamos que la intensidad de la interacción entre las hormigas soldado y las aves seguidoras de hormigas, obligadas o facultativas, predice el traslape de las áreas de distribución de las especies que interactúan, así como la extensión de las áreas de distribución. Generamos modelos de distribución de especies con MAXENT y estimamos el porcentaje de traslape entre dos especies de hormigas soldado y diez especies de aves seguidoras de hormigas. Contrario a nuestras predicciones, los modelos de regresión Bayesiana no apoyaron un mayor traslape

de áreas entre las aves obligadas seguidoras de hormigas y las hormigas soldado o áreas de distribución más amplias para las especies de aves facultativas seguidoras de hormigas. Sin embargo, nuestros resultados sugirieron tendencias; los porcentajes de traslape de áreas de distribución fueron más altos entre las aves obligadas seguidoras de hormigas y las hormigas soldado y las áreas de distribución de las aves facultativas seguidoras de hormigas fueron más amplias, extendiéndose a áreas sin la presencia de hormigas soldado. Nuestra investigación incentiva más exploración de la biogeografía de interacciones bióticas como parte de un gradiente cuantitativo de intensidades en lugar de categorías cualitativas, integrando la variación espacial y temporal en la intensidad de interacción.

Key words: Biogeography, biotic interactions, facultative, obligate, parasitism, range overlap

Palabras clave: Biogeografía, facultativa, interacciones bióticas, obligada, parasitismo, traslape de área

Introduction

Understanding the interactions that help determine the geographic ranges of species is a central topic in biogeography (Brown et al. 1996). Range distributions result from the interactions of evolutionary history, abiotic factors, and biotic interactions (Soberón and Nakamura 2009; Wiens 2011). Research from the past two decades consistently incorporates evolutionary history (e.g., modeling an evolutionary independent unit in a region that has been accessible to its dispersal or colonization) and abiotic factors (e.g., scenopoetic variables) when predicting and delimiting geographic ranges of a variety of terrestrial and aquatic species. However, our comprehension of the biotic interactions that determine geographic ranges and the spatial scale at which they are relevant is still limited (Wiens 2011; Anderson 2017). Moreover, the geography of biotic interactions and their intensity can be influenced by behavior (Marske et al. 2023), a combination of variables of special concern for biological conservation, mainly when the interacting species represent key links in the ecosystems of which they are a part (e.g., army ants in Neotropical ecosystems). We aim to study the biogeography of biotic interactions, specifically, those interactions, the intensity of which are influenced by behavior.

Biotic interactions are grouped into different categories based on whether the outcome is positive, negative or neutral for the species involved; additionally, species interactions can vary in intensity and be classified, for instance, as obligate or facultative, and as specialist or generalist. Evidence and theoretical expectations suggest that the overlap between geographic ranges of interacting species may predict diverse patterns, which can vary or recur among the different categories of interactions (Araújo and Rozenfeld 2014; Fig. 1). For instance, high levels of competition between a pair of species lead to geographic exclusion where ranges can abut but not overlap, while lower levels of competition allow for geographic overlap (Anderson et al. 2002; Wiens 2011; Fig. 1A). Predation (including the following interactions: predator/prey, parasite/host, herbivore/plant, Batesian mimic/model) can limit the ranges of the predator and the prey in different ways (Sexton et al. 2009; Wisz et al. 2013), when the predator is obligate (specialist) its range will be limited to the geographic range of the prey, although the prey can have a wider range than the predator; but when the symbiotic relationship is facultative (generalist) different amounts of range overlap between the predator

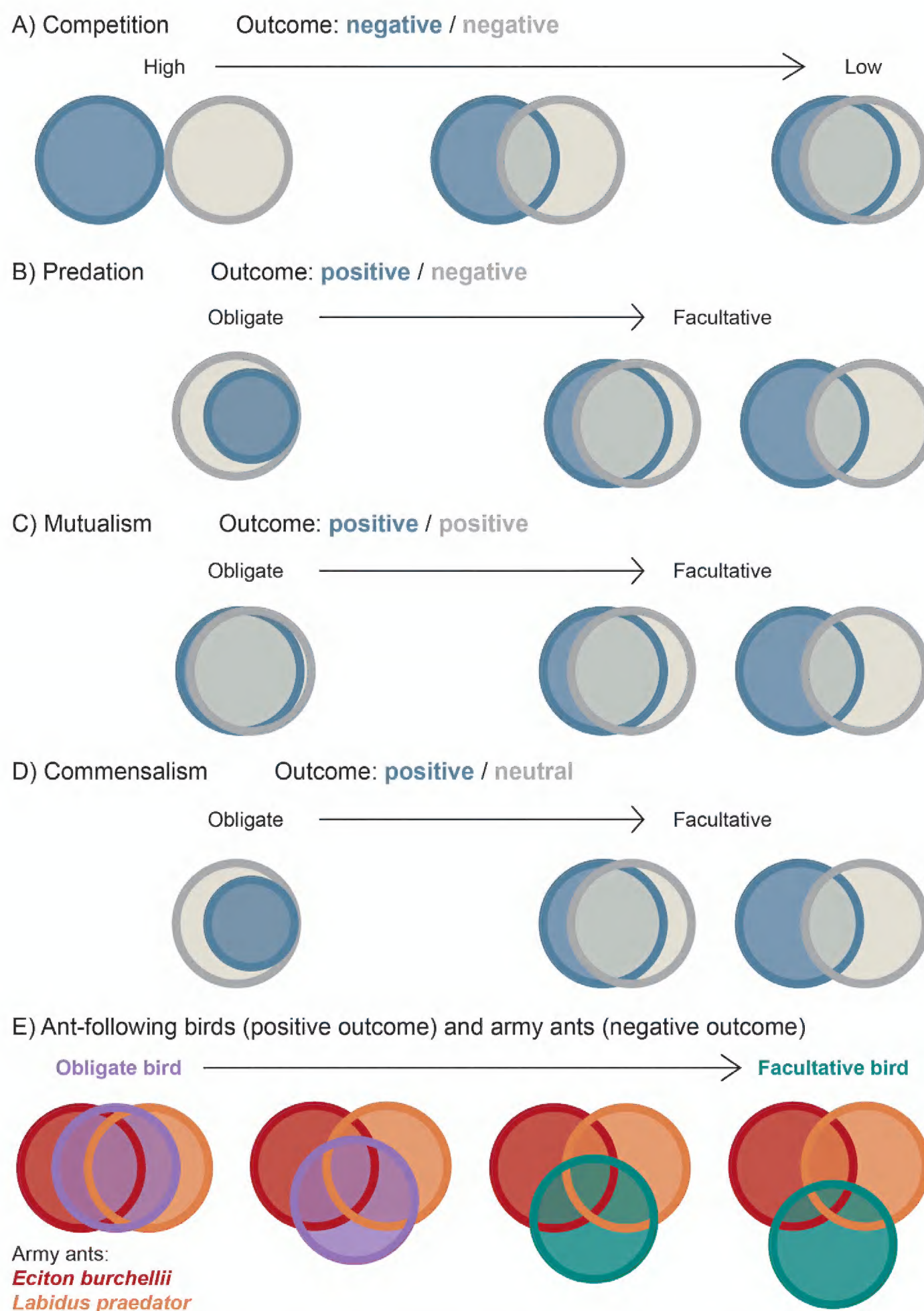


Figure 1. Biogeography of biotic interactions. Expected overlap of the geographic ranges of interacting species, considering different kinds of interactions and intensities of the interactions **A** competition: both competing species have a negative outcome and with high levels of competition exclude each other geographically **B** predation: one species has a positive outcome (blue) and the other species has a negative outcome (gray) as in the interactions predator/prey, parasite/host, herbivore/plant, Batesian mimic/model **C** mutualism: both interacting species have a positive outcome and (almost) complete geographic overlap is expected when the interaction is obligate **D** commensalism: one species has a positive outcome (blue) and the other species is neutral (gray) **E** higher range overlap is expected between obligate ant-following bird species and army ants than between facultative ant-following bird species and army ants.

and a particular species of prey are expected, in this case the geographic range of the predator will overlap with multiple prey species (Holt and Barfield 2009; Sexton et al. 2009; Wisz et al. 2013; Araújo and Rozenfeld 2014; Fig. 1B). Mutualism, as an interspecific interaction in which the species involved have a posi-

tive outcome, complete overlap on geographic ranges of interacting species is expected when there is an obligate relationship, and different amounts of range overlap when there is a facultative relationship (Stephan et al. 2021; Fig. 1C). In commensalism, a complete range overlap is expected in an obligate commensal species although the host can have a wider range, and different amounts of range overlap when there is a facultative relationship (Stephan et al. 2021; Fig. 1D). The recurring geographic patterns, mainly in facultative interactions, and the variation in the intensity (obligate vs. facultative) of the interactions make it more difficult to comprehend how species interactions at the local/ecological scale relate to geographic ranges at the regional scale, especially when the limits of the geographic ranges of the interacting species have not been defined.

Species distribution models (SDMs) are used to predict the potential geographic ranges of the species of interest, mainly based on occurrence data and environmental (abiotic) variables (Elith et al. 2011; Wiens 2011; Wisz et al. 2013). Recently, the practice of modeling including biotic interaction variables and understanding which variables (abiotic or biotic) contribute more to the distribution model of the species of interest has increased (Meier et al. 2010; Giannini et al. 2013; Pellissier et al. 2013; Atauchi et al. 2018; Thompson et al. 2020). Biotic variables, in general, improve predictions (Meier et al. 2010; Pellissier et al. 2013; de Araújo et al. 2014; Thompson et al. 2020), falsifying the Eltonian Noise Hypothesis (ENH) that indicates that local/ecological scale biotic interactions do not have an effect on distribution areas at regional scales (Soberón and Nakamura 2009). Additional examples (not all of them based on SDMs) of the important role that biotic interactions play in geographic ranges at broad spatial scales can be found in the literature (Wisz et al. 2013 and references therein); although results supporting the ENH have also been reported (Fraterrigo et al. 2014). Prior knowledge of the ecology of the species under study, including interspecific interactions, has been pointed out as necessary to improve our understanding of how local interactions affect regional geographic ranges (Wisz et al. 2013; Anderson 2017); a way to do this can be considering species with interspecific interactions in different intensities.

The effect of the intensity of interspecific interactions in determining geographic ranges has been barely explored. To date, results show that SDMs are not differently affected by the inclusion of biotic variables in both, dietary generalist and specialist species (de Araújo et al. 2014), which is contrary to expectations. Populations of specialist species are expected to be strongly affected by their interactors, and therefore, specialist species SDMs are expected to perform better when incorporating biotic predictor variables related to generalist species SDMs (Anderson 2017). To avoid the differences that incorporating biotic variables are expected to generate in the SDMs of species that interact at different intensities, another approach consists in building the models of each of the species independently and subsequently overlapping the SDMs of the interacting species and measure how much of the interaction can be captured by the percentage of overlap. We follow that approach to explore the geographic ranges of army ants and parasitic ant-following birds.

Army ants are mainly tropical species that inhabit forested areas of North America (Fisher and Cover 2007), Central America, South America, and Africa (Willis and Oniki 1978). Army ants play an important role in the dynamics of the ecosystems given that they predate large amounts of arthropods and many species of animals benefit from feeding on arthropods that try to escape from the

ants (Willis and Oniki 1978; Kaspari and O'Donnell 2003; Kronauer 2009). The animal species that benefit from escaping arthropods may change across ant geographic ranges and also the timing (time of day and year) that ants are active and in foraging behavior (Willis and Oniki 1978). Most species of army ants feed during the night, although two species of Neotropical ants are known to feed during the day, *Eciton burchellii* and *Labidus praedator* (Kaspari and O'Donnell 2003; Kronauer 2009). Diurnal feeding behavior allows for birds to benefit from interactions with the army ants (Willis and Oniki 1978). The interaction between army ants and ant-following birds is considered parasitism because the birds reduce the ants' success rate in capturing prey (Wrege et al. 2005).

Ant-following birds are highly diverse in the Neotropics, encompassing several orders and about 41 families (Willis and Oniki 1978; Martínez et al. 2021) across a wide range of elevation (i.e., from sea level to ~3000 m asl). More than 30 species of ant-following birds can swarm around a large ant colony (Willis and Oniki 1978; O'Donnell 2017). Ant-following birds can vary in the specialization of ant-following behavior; this behavior can be obligate or facultative. Obligate ant-following birds need to follow the ant raids as they appear incapable of foraging if their prey is not flushed by the ants (Brumfield et al. 2007); few families of birds, including *Thamnophilidae* and *Furnariidae* are obligate followers. Facultative ant-following birds feed opportunistically when army ants move through their territory; this category of specialization of ant-following behavior also includes ant-followers that regularly chase army ants beyond their territory, but also feed independently of the ants (Willis and Oniki 1978; O'Donnell 2017). The study of the biogeography of bird species that vary in the specialization of ant-following behavior was recently highlighted as a research opportunity to advance our understanding of ant-followers (Martínez et al. 2021), and the authors suggest that ant-following behavior is geographically constrained by the presence of swarming army-ant species.

Here, we explore the biogeography of the interspecific interactions of parasitism between army ants and obligate and facultative ant-following birds. We contrast SDMs of two species of army ants against SDMs of five species of obligate ant-following birds and five species of facultative ant-following birds. Our hypothesis is that the intensity of the interaction between army ants and ant-following birds (obligate vs. facultative) is reflected in the overlap of geographic ranges between the army ants and the birds. Therefore, we predict that obligate ant-following birds show a higher overlap with the geographic range of army ants than facultative followers (Fig. 1E), given the strong behavior of following ants to feed. Complementarily, facultative ant-following birds can have wider geographic ranges than obligate followers because they can extend geographically to areas with no army ants. As far as we know, our study represents the first attempt to quantify the biogeography of army ants and ant-following birds at a regional scale.

Methods

Study region

Our study region encompassed the northern Neotropics, from Mexico to the Darién Gap at the Panama-Colombia border. The northern limit of our study region corresponds with the Mexican Transition Zone (MTZ), which is located in

the overlap between the Nearctic and Neotropical regions. The MTZ represents a natural biogeographic barrier for many Neotropical taxa (Morrone 2020), including the ant species and most of the bird species covered in our study. The Darién Gap is the region that connects Central and South America and corresponds with geographic limits of a wide taxonomic range of taxa (Daza et al. 2010; Smith et al. 2014; Winston et al. 2017). The study region is recognized as a biogeographic region that matches the geographic distribution of monophyletic groups, both of army ants (e.g., *Eciton burchellii*, Winston et al. 2017) and lowland Neotropical birds (Smith et al. 2014). Therefore, our study region offers the opportunity to study the biogeography of interspecific interactions, parasitism specifically, taking into account the evolutionary history of the different taxa involved.

Bird and army-ant species included in this study

To test our hypothesis that the intensity of the interaction is reflected in the overlap of geographic ranges between army ants and ant-following birds, we analyzed the geographic ranges of two species of army ants and ten species of ant-following birds. We selected the two species of army ants that represent most of the army ant swarms in the region, *Eciton burchellii* and *Labidus praedator* (Coates-Estrada and Estrada 1989; Martínez et al. 2021). We also selected five obligate and five facultative ant-following bird species (Table 1) based on our own observations (NDMR, PG, RAJ) and the literature (Willis and Oniki 1978; Coates-Estrada and Estrada 1989; Swartz 2001; Chaves-Campos 2003; Greeney et al. 2020).

Downloading data from the web

We used presence data points available in digital public repositories to build species distribution models for each study species. We downloaded data for all species (ants and birds) from the Global Biodiversity Information Facility (GBIF). Specifically, we downloaded data restricted to our study region (Mexico

Table 1. Species of army ants and ant-following birds analyzed. Data points to generate species distribution models were downloaded from the Global Biodiversity Information Facility (GBIF); the number of data points downloaded varied by species, as well as the number of data points included in the models after filtering.

Species	GBIF data points downloaded	GBIF data points included	GBIF hyperlink
Army ants			
<i>Eciton burchellii</i>	2541	202	https://doi.org/10.15468/dl.svptv7
<i>Labidus praedator</i>	1034	273	https://doi.org/10.15468/dl.ghepdn
Obligate ant-following birds			
<i>Gymnopithys bicolor</i>	42	16	https://doi.org/10.15468/dl.2js9kq
<i>Phaenostictus mcleannani</i>	78	38	https://doi.org/10.15468/dl.xqb8wz
<i>Dendrocincla anabatina</i>	567	219	https://doi.org/10.15468/dl.rcrmwc
<i>Dendrocolaptes sanctithomae</i>	143	86	https://doi.org/10.15468/dl.cdnvpv
<i>Eucometis penicillata</i>	512	196	https://doi.org/10.15468/dl.x38dw9
Facultative ant-following birds			
<i>Attila spadiceus</i>	1025	536	https://doi.org/10.15468/dl.ux84ud
<i>Sittasomus griseicapillus</i>	1225	472	https://doi.org/10.15468/dl.bs4g6
<i>Ramphocaenus melanurus</i>	485	275	https://doi.org/10.15468/dl.mm5vzs
<i>Henicorhina leucosticta</i>	1319	391	https://doi.org/10.15468/dl.tgrjnw
<i>Habia fuscicauda</i>	1947	517	https://doi.org/10.15468/dl.awjz3k

to Panama), that were records of specimens belonging to biological collections, and that included geographic coordinates. To supplement the data points for one of the bird species (*Gymnopathys bicolor*), we added 20 records from The Macaulay Library (ML). From the ML, we selected records that included photographic evidence of the bird to confirm species identification. All GBIF and ML citations are available in Table 1, 2, respectively.

Data filtering

We filtered the GBIF presence data points to obtain a final reduced and revised set of points for each species. First, we removed duplicate presence points with the same geographic coordinates. We then visualized the data points on a map to verify that they were all located on continental land and within our study region. Finally, we removed data points that placed the specimen records outside of continental land (i.e., in the ocean). The final number of presence data points for each species analyzed is reported in Table 1.

Species distribution modeling

We built species distribution models (SDMs) to explore the overlap between the geographic ranges of army ants and ant-following birds. We modeled the potential distribution range for each of the two army ant species and the ten ant-following birds in our study region.

We built the SDMs using the maximum entropy algorithm implemented in MAXENT v. 3.4.1 (Phillips et al. 2006; Phillips et al. 2023), presence data points (as described above), and current environmental conditions. For the environmental conditions, we used uncorrelated sets of the standard 19 bioclimatic variables downloaded from WorldClim (Fick and Hijmans 2017; <https://www.worldclim.org/data/worldclim21.html>) at 30-arc second resolution. To select the uncorrelated set of bioclimatic variables, we did as follows for each species separately: (i) we extracted the climatic data for each individual presence point, (ii) tested for significative correlation ($p > 0.05$) among the 19 variables, and (iii) selected the most temporally inclusive variable for each pair of correlated variables (> 0.9 Pearson correlation coefficient). The final set of variables used to build the SDM for each species varied between 9 and 15 variables (Suppl. material 1: table S1). Finally, we built a SDM for each species using the default

Table 2. *Gymnopathys bicolor* geographic records from The Macaulay Library (ML) included in this study for generating the species distribution model.

No.	ML catalog number	No.	ML catalog number
1	ML31564301	11	ML555722431
2	ML33712981	12	ML559050011
3	ML47880731	13	ML565958121
4	ML53591581	14	ML566216821
5	ML72199371	15	ML572564301
6	ML108049151	16	ML576572301
7	ML287666611	17	ML580064621
8	ML544000281	18	ML580193821
9	ML551267121	19	ML582128301
10	ML552367261	20	ML583306691

convergence threshold (10^{-5}) and 500 iterations (Pearson et al. 2007). Each modeling analysis was set to randomly use 75% of the presence points for training and 25% for testing the model. From the default advanced settings, we unselected the option “Do clamping.” We checked the AUC statistic to assess model performance (Metz 1978). AUC values should be higher than 0.5 for the model to be better than random, although as values approach more to 1, the better the model predicts the presence of the taxon of interest (Phillips 2017). However, we were aware that AUC statistics can have artifacts, for instance, AUC values tend to be higher for species with narrow ranges, relative to the study geographic/environmental area, without meaning that the models are better (Phillips 2017).

Overlap between geographic ranges between army ants and ant-following birds

We reclassified the SDMs as presence/absence and calculated the overlap between each species of army ants against each species of ant-following bird. Using geographic information system software, we reclassified the presence probability values of the SDMs into presence and absence values (i.e., 1 and 0, respectively). We defined as presence all values above the logistic threshold for the “10 percentile training presence” as indicated in the MAXENT results; any value equal to or less than that threshold was considered as absence. Then, we proceeded to estimate the percentage of overlap between geographic ranges of army ants and ant-following birds. To test our predictions, we were specifically interested in quantifying the geographic range occupied by each species and how much of the geographic range of each species of ant-following bird overlaps with the distribution range of the army ants, both, separately by each one of the two species of army ants and combined as any species of army ants. We expected obligate ant-following birds to show a higher overlap with the geographic range of army-ants than facultative followers, and facultative ant-following birds to have wider geographic ranges than obligate followers.

Statistical analysis: overlap between obligate vs. facultative ant-following birds

We assessed how much percentage overlap in the distribution of birds and ants occurs due to the intensity of the interaction (i.e., obligate ant-following birds vs. facultative ant-following birds) using a Bayesian regression model (Bürkner 2017; Gelman et al. 2020). Model took the form:

$$P = B_0 + X_i B_1$$

where P is overlap proportion among bird and ants, X_i is a categorical predictor identifying obligate ant-following bird species. B_0 is a predicted parameter of overlap proportion of facultative ant-following bird species, and B_1 is a parameter of variation on predicted overlap proportion if bird is an obligate ant-following bird species. Bayesian regression models were fit using Beta distribution, given that data are proportions, in the “brms” package in R (Bürkner 2017; Core Team R 2017). Implementing a Bayesian regression model allows us to estimate the variation on parameters B_0 and B_1 .

We also evaluated how much larger areas were estimated in the SDMs due to the intensity of the interaction using a Bayesian robust regression model, given area is a continuous variable (Bürkner 2017; Gelman et al. 2020). Models took the form:

$$A = B_f + X_i B + \epsilon$$

where A is the estimated area (km^2), and X_i is a categorical predictor identifying obligate ant-following bird species, as before. B_f is a predicted parameter of estimated area of facultative ant-following bird species, and B is a parameter of variation on predicted estimated area if the bird is an obligate ant-following bird species. ϵ is t-distributed error of the model. Robust regression models were fit using Student family in the “brms” package in R (Bürkner 2017; Core Team R 2017), so coefficient estimated were less influenced by outliers.

We ran simulations to the posterior distributions on four Markov Chain Monte Carlo (MCMC). MCMC sampling of posteriors was performed in 1000 iterations by chain after 3000 warm-up iterations. We visually checked chain convergence and the scale reduction factor, R-hat < 1.1, for all parameters.

Results

We employed species distribution models (SDMs, AUC values higher than 0.831, Suppl. material 1: table S2) and Bayesian regression models in order to better understand the biogeography of interspecific interactions between ant-following birds and the army ants *Eciton burchellii* and *Labidus praedator*. Our hypothesis was that the intensity of the interaction between army ants and ant-following birds (obligate vs. facultative) is reflected in the percentage of overlap of geographic ranges between the army ants and the birds. Contrary to expectations from the hypothesis, our results did not show an estimated higher overlap between obligate ant-following birds and army ants when compared to facultative ant-following birds (Fig. 2A). However, obligate ant-following birds had the maximum overlap values (mean = 88%; C.I. = 77%, 94%), and facultative ant-following bird species had the minimum overlap values (mean = 79%; C.I. = 66%, 87%) with the potential geographic range of army ants (Table 3). Our results also did not show evidence supporting the second prediction (Fig. 2B), although facultative ant-following bird species tend to have wider expected geographic ranges (mean = 6613 km^2 ; CI = 4440 km^2 , 8827 km^2) than expected geographic ranges of obligate ant-following birds (mean = 3720 km^2 ; CI = 1523 km^2 , 6016 km^2).

We noticed a trend of increased overlap between the geographic ranges of army ants and ant-following birds in relation to behavior, obligate ant-following birds showed higher overlap than facultative ant-following birds (Figs 3, 4), even though there is no statistical difference. Among the species of birds with obligate ant-following behavior, the percentage of overlap with *E. burchellii* was between 84.60% (*Gymnopithys bicolor*) and 68.33% (*Dendrocolaptes sanctithomae*); whereas the percentage of overlap with *L. praedator* varied between 79.01% (*Eucometis penicillata*) and 57.16% (*G. bicolor*). The birds with facultative ant-following behavior showed percentages of overlap with *E. burchellii* between 76.23% (*Henicorhina leucosticta*) and 53.44% (*Attila spadiceus*); whereas the percentage of overlap with *L. praedator* varied between 73.65% (*H. leucosticta*) and 48.83% (*A. spadiceus*).

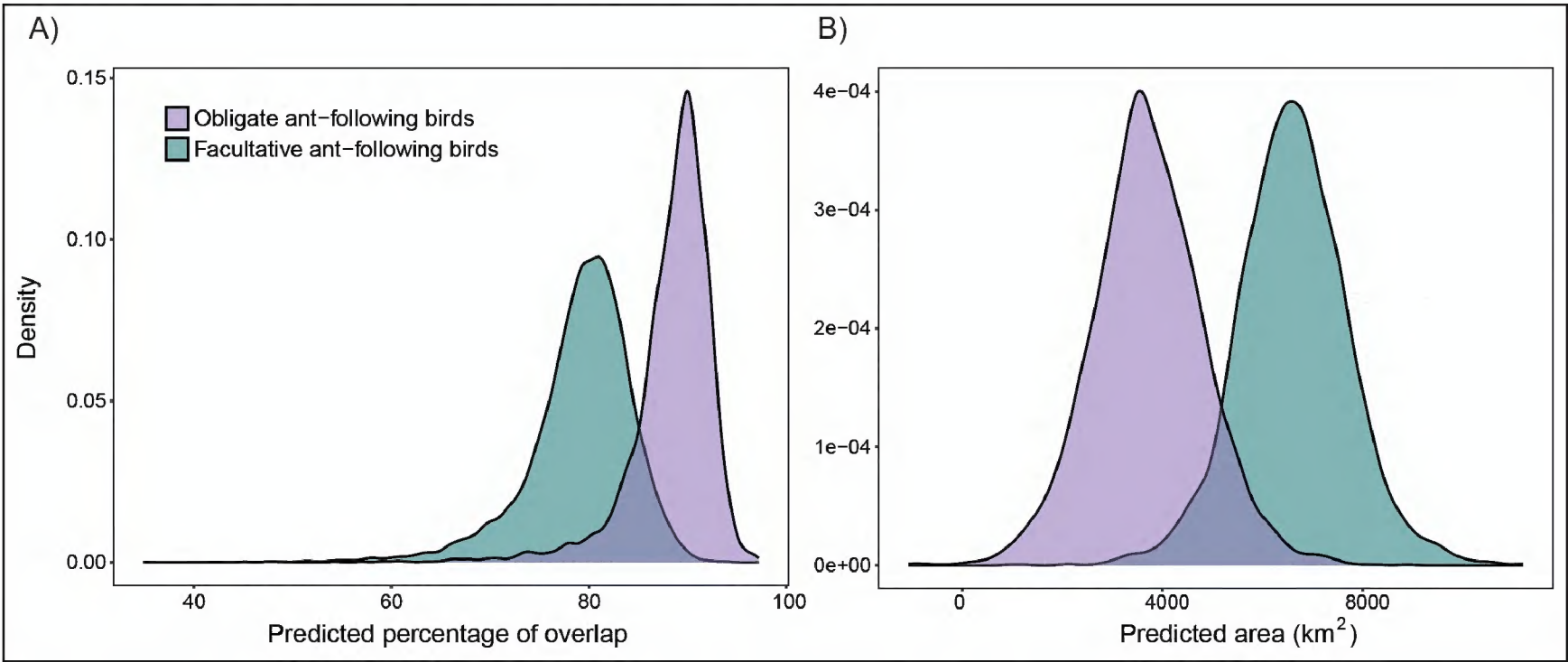


Figure 2. Bayesian regression models show that the intensity of the interaction between army ants and ant-following birds (obligate vs. facultative) is not reflected in the overlap of geographic ranges between the army ants and the birds **A** obligate ant-following birds do not have higher estimated overlap of geographic ranges than facultative ant-following birds **B** facultative ant-following birds do not have wider expected geographic ranges than obligate ant-following birds.

Table 3. Percentage of overlap between army ants and ant-following birds and predicted range size by Species Distribution Models (SDM) in square kilometers.

Species	% of overlap between bird and <i>Eciton burchellii</i>	% of overlap between bird and <i>Labidus praedator</i>	% of overlap among bird and two ants	Predicted area size by SDM (km ²)
Obligate ant-following birds				
<i>Gymnopithys bicolor</i>	84.60	57.16	88.44	2136
<i>Phaenostictus mcleannani</i>	80.86	64.04	87.12	1902
<i>Dendrocincla anabatina</i>	69.17	76.71	92.28	4479
<i>Dendrocolaptes sanctithomae</i>	68.33	59.36	83.72	7524
<i>Eucometis penicillata</i>	73.90	79.01	96.84	2977
Facultative ant-following birds				
<i>Attila spadiceus</i>	53.44	48.83	67.19	9415
<i>Sittasomus griseicapillus</i>	58.90	62.81	78.22	7075
<i>Ramphocaenus melanurus</i>	66.00	68.75	88.05	4150
<i>Henicorhina leucosticta</i>	76.23	73.65	88.23	5940
<i>Habia fuscicauda</i>	63.56	60.17	80.93	6525

However, since the geographic ranges of ant species complement each other, the total overlap between birds and army ants increased, ranging from 96.84% (*E. penicillata*) to 83.72% (*D. sanctithomae*) in obligate ant-following birds, and 88.23% (*H. leucosticta*) to 67.19% (*A. spadiceus*) in facultative ant-following birds.

Coinciding with our prediction, there was a trend for the geographic ranges of facultative bird species to be more extensive. We observed that facultative ant-following birds extended their distribution to areas where no army ants were predicted (Figs 3, 4), which is also reflected in lower percentages of overlap between army ants and facultative ant-following birds (Table 3). For example, *A. spadiceus* extended its distribution area along the pacific slope of Mexico, where it does not overlap with any of the studied army ants species.

Both obligate and facultative ant-following behaviors presented three out of five bird species with a higher percentage of overlap with *E. burchellii* than

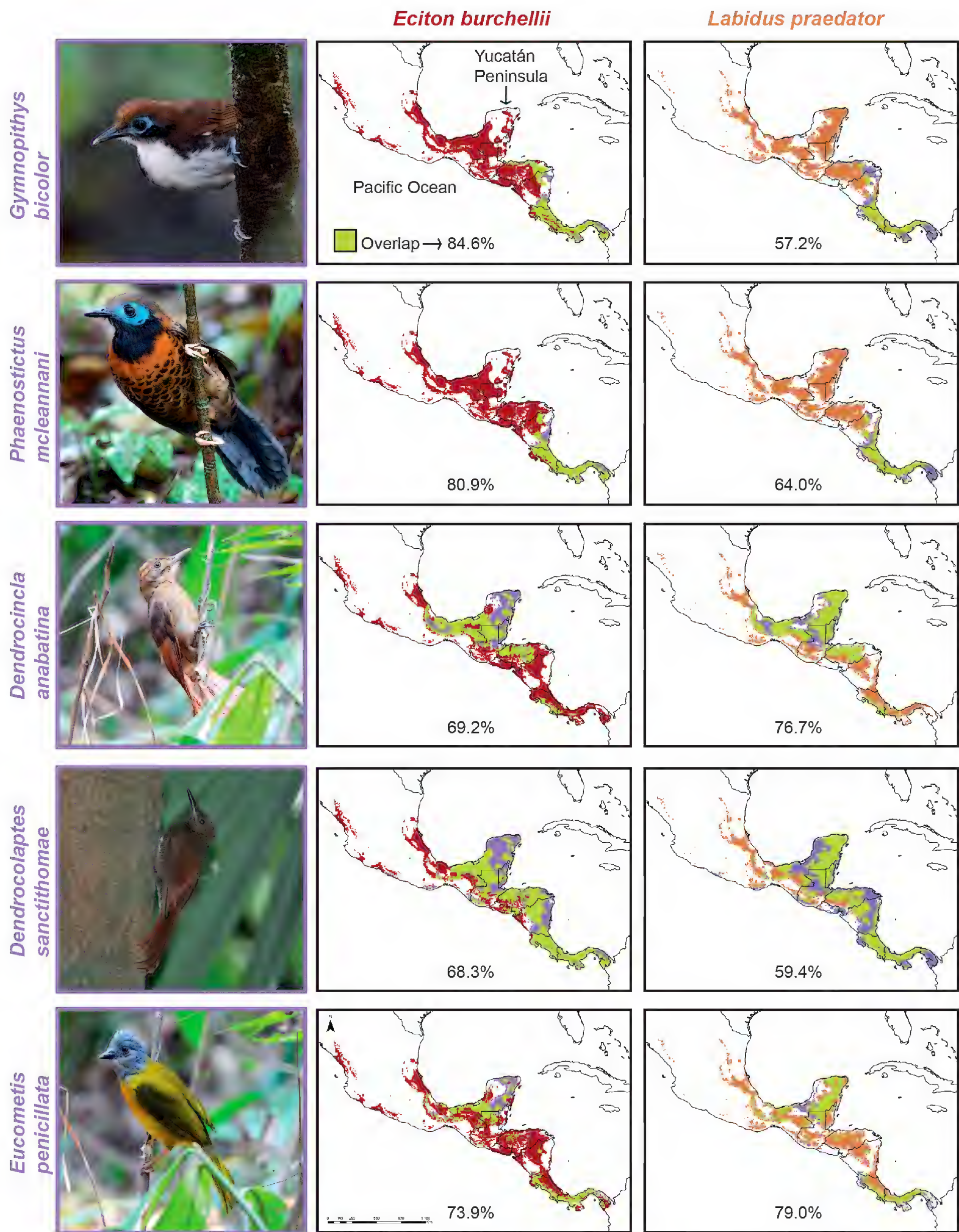


Figure 3. Overlap of species distribution models of two species of army ants (columns; *Eciton burchellii*, carmine color, and *Labidus praedator*, caramel color) and five species of obligate ant-following birds (rows, amethyst color). Range overlap between army ants and ant-following birds is shown in lime color, and the percentage of overlap is represented numerically for each ant-bird species pair. Photo credits: *G. bicolor* (Melton 2023a), *P. mcleannani* (Melton 2023b), *D. anabatina* (NDMR), *D. sanctithomae* (PG), *E. penicillata* (NDMR).

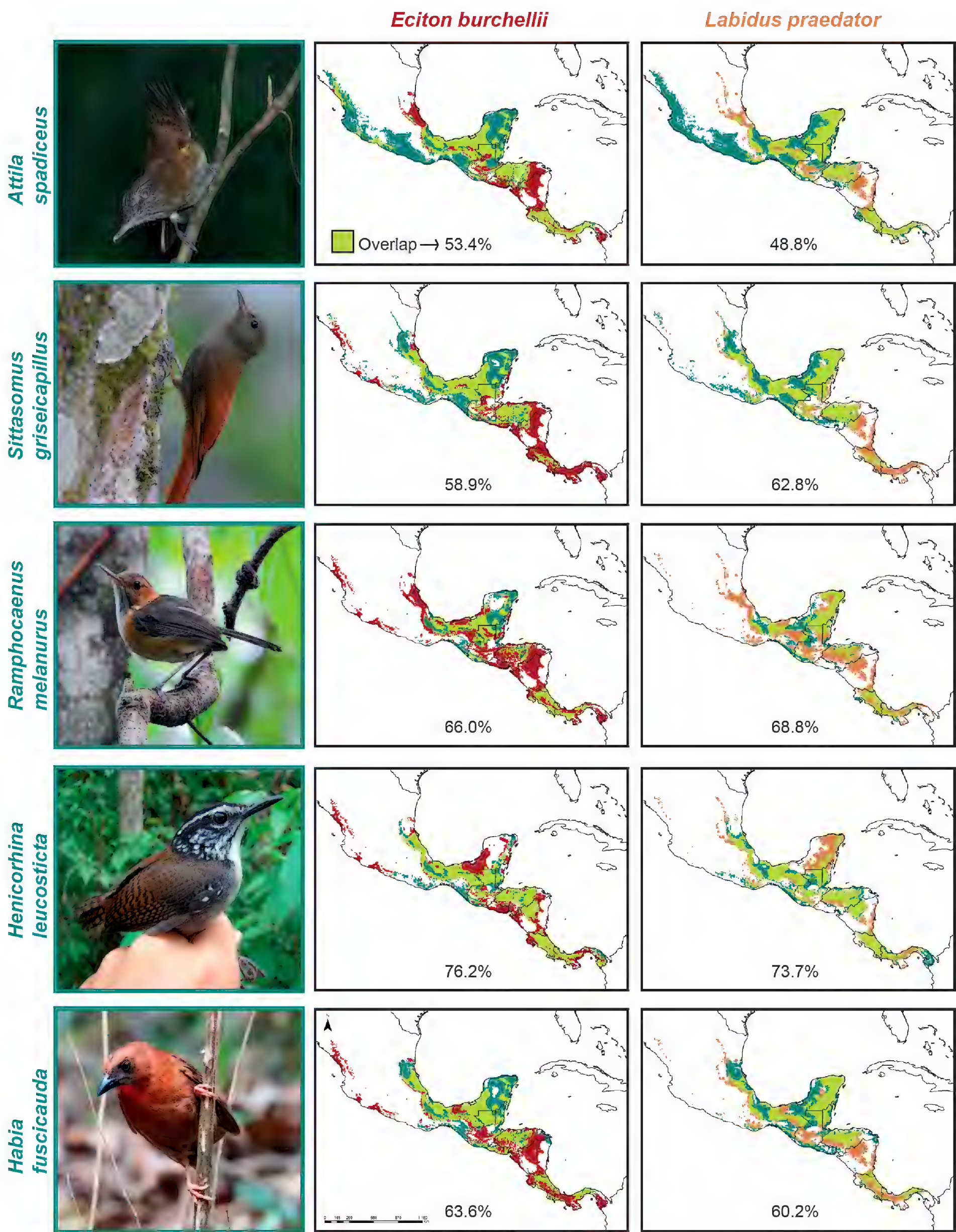


Figure 4. Overlap of species distribution models of two species of army ants (columns; *Eciton burchellii*, carmine color, and *Labidus praedator*, caramel color) and five species of facultative ant-following birds (rows, teal color). Range overlap between army ants and ant-following birds is shown in lime color, and the percentage of overlap is represented numerically for each ant-bird species pair. Photo credits: *A. spadiceus* (PG), *S. griseicapillus* (Carlos Echeverría), *R. melanurus* (NDMR), *H. leucosticta* (RAJ), *H. fuscicauda* (NDMR).

with *L. praedator*. The higher percentages of overlap of obligate birds with *E. burchellii* were 84.60% (*G. bicolor*), 80.86% (*P. mcleannani*), and 68.33% (*D. sanctithomae*); and in the facultative birds the values were 76.23% (*H. leucosticta*), 66.00% (*Ramphocaenus melanurus*), and 63.56% (*Habia fuscicauda*).

Although the geographic ranges of *E. burchellii* and *L. praedator* are different, they complemented each other in the study region (Figs 3, 4). The range of *E. burchellii* covers a larger area (7619 km²) than the range of *L. praedator* (6383 km²). The main differences between the two ant species are observed in the Yucatán Peninsula and the pacific slope. Specifically, in the Yucatán Peninsula, *E. burchellii* is replaced by *L. praedator*. These differences in the geographic ranges promote the overlap of ant-following birds and army ants, resulting in an increase in the total percentage of overlap when considering a bird species and the two army ant species (Table 3), especially when the geographic range of the birds encompasses the Yucatán Peninsula.

Discussion

We studied the biogeography of interspecific interactions between army ants and obligate and facultative ant-following birds. We hypothesized that the intensity of the interaction between army ants and ant-following birds would determine the percentage of overlap of the geographic ranges of the interacting species. Contrary to our first prediction, a Bayesian regression model found no support for an estimated higher range overlap between obligate ant-following birds and army ants when compared to facultative followers, which agrees with Eltonian Noise Hypothesis (Soberón and Nakamura 2009), the intensities of interactions defined at the local scale are weakly reflected in the percentage of overlap of geographic ranges at the regional scale. Regarding our second prediction, the Bayesian regression model showed that the studied species of facultative ant-following birds do not have wider geographic ranges than the obligate followers, although there was a trend for facultative species to extend geographically to areas with no army ants. Our study contributes to the understanding of regional scale biogeography of species interactions, specifically when there are differences in the intensity of interactions, a component that has been little integrated in this field of research.

Species interactions between army ants and ant-following birds integrate complex networks, both on the number and identity of the species in a given local assemblage and on the environmental factors that limit geographic ranges throughout their extent, which can alter the intensity of the interactions (Early and Keith 2019). Species of ant-following birds can switch from facultative where other species of obligate followers are present and abundant to obligate where those other obligate followers are absent (Touchton and Smith 2011; Martínez et al. 2021). For instance, in the absence of *Phaenostictus mcleannani*, a species with strongly obligate ant-following behavior, it has been observed that other bird species can increase their obligate behavior (Touchton and Smith 2011). Biotic interactions are known factors that limit geographic ranges, especially when there is high level of competition between species, however the role of predation (including parasitism) in limiting geographic ranges has received conflicting support (Sexton et al. 2009). Our results suggests that for the interaction of parasitism between army ants and ant-following birds, the ranges of bird species considered to have obligate ant-following behavior may extend to plac-

es where the army ants *E. burchellii* and *L. praedator* are not predicted to live (i.e., obligate ant-following birds do not have an overlap of 100% with the geographic ranges of any studied species of army ants). These results lead us to propose two alternatives: 1) in those places the birds follow another species of army ant not considered in this study, as found in the Yucatán Peninsula, the complementarities of the distribution areas of ant species may favor bird species to distribute more widely, interacting with *E. burchellii*, *L. praedator*, or both ant species; 2) the birds are not as obligate as is thought, obligate and facultative are two categories that may not accurately represent the intensity of interactions; another way of referring to obligate species has been proposed, obligate species can be referred to as “professional” ant-followers when they obtain more than 50% of their meals from army ant swarms (Willis and Oniki 1978; Swartz 2001).

The classification of ant-following behavior into two categories, obligate and facultative, eliminates the gradient of the intensity of the interactions, which may have implications in determining the overlap of geographic ranges of ant-following birds and army ants. Our results of the Bayesian analysis of the estimated percentage of overlap of the geographic ranges between ants and birds show a region of intersection between both categories of intensities, challenging the classification commonly used in this field of research and showing that there is no defined threshold between obligate and facultative species (Willson 2004). Previous studies have shown that although bird species have facultative behavior, some of these species can be opportunistic and follow bird species with obligate behavior (e.g., *Henicorhina leucosticta* and *Habia fuscicauda* are known to follow the call of *P. mcleannani*) to take advantage of food availability, which may have an effect on the geographic areas of facultative species, obscuring the division between categories and resulting in the observed intersection between both categories of intensities (Chaves-Campos 2003). Moreover, interspecific variation, resulting from differences in the evolutionary history, body size, territorial and foraging behavior of birds (Pizo and Melo 2010; Martínez et al. 2021), also has effects on how geographic ranges are shaped; for instance, our results suggest that bird species with facultative behavior can extend their distribution to places where the army ants *E. burchellii* and *L. praedator* are not present, as was evidenced by *A. spadiceus*. Finally, intraspecific variation is an important factor to take into account when performing biogeographic analysis since the category to which a certain species is assigned can vary when considering different sites throughout the distribution area (Stephan et al. 2021); making it difficult to move from the local scale to the regional scale.

Bird species are assigned as obligate or facultative based on local scale field studies and with our study, we attempted to transfer that local scale natural history information to the percentage of overlap between geographic ranges at the regional scale. Our findings show no support for an estimated higher range overlap between obligate ant-following birds and army ants when compared to facultative followers. The lack of support for our predictions leads us to propose that Eltonian Noise Hypothesis might partly explain our results (de Araújo et al. 2014). However, this does not mean that the biotic interactions documented at a local scale do not have an effect on distribution areas at a regional scale in the study system, since a trend towards greater area overlap was observed in species classified as obligate. It has been demonstrated in previous studies that biotic interactions do play a role in defining geographic ranges at regional

scales (Soberón and Nakamura 2009; Wiens 2011; Wisz et al. 2013), and therefore, we do not rule out the possible influence of interactions between birds and ants in determining the overlap of distribution areas. We want to highlight that this trend was possible to detect thanks to the fact that our study included the analysis of 10 species of birds, highlighting the importance of studying the biogeography of biotic interactions in multiple species at the same time.

As mentioned previously, the categorical classification of the intensity of interactions hides the intensity gradient over which interactions can occur, and the local spatial scale at which the intensity of interaction is determined adds up to the difficulty of moving from the local scale to the regional scale. Thus, an alternative explanation for our results is that the categories evaluated (i.e., obligate vs. facultative) do not allow the integration of quantitative values of the intensity of interaction to be able to study the overlap of geographic ranges in a continuous and non-categorical manner, and consider spatial and temporal intraspecific variation. It would be valuable to incorporate, in biogeographic studies, the spatial intraspecific variation that results from different assemblages and environments, since a bird species inhabiting different regions (e.g., Central America vs. Amazonia) can show differential intensity of ant-following behavior. Given these challenges in understanding and categorizing interaction intensities, it is essential to consider the spatial variation in interaction intensity of particular species, for instance *Henicorhina leucosticta* and *Habia fuscicauda*, two bird species generally considered as facultative ant-followers. Individuals of *H. leucosticta* join *E. burchellii* swarms in Los Tuxtlas, Mexico with a frequency of 57% (Coates-Estrada and Estrada 1989), while in Costa Rica this bird species shows a visitation frequency of 31% to *E. burchellii* swarms (Chaves-Campos 2003), and in general, *H. leucosticta* is not considered a true swarm-follower (Kroodsma and Brewer 2020). Similarly, *H. fuscicauda* is the bird species with the highest attendance at swarms of two species of army ants, *E. burchellii* and *L. praedator*, in Los Tuxtlas, Mexico (Coates-Estrada and Estrada 1989), while in the Yucatán Peninsula *H. fuscicauda* was recorded as an occasional swarm-follower (Willis 1960).

Temporal variation in assemblages should also be incorporated, particularly in bird assemblages that go through an annual cycle with a season of residents-only and a season of resident and migratory species, since some migratory birds (e.g., *Geothlypis formosa* – Kentucky Warbler, *Setophaga citrina* – Hooded Warbler) can also join the mixed species flocks of ant-following birds in Guatemala (observations by NDMR) and Mexico (Coates-Estrada and Estrada 1989), and although it has been proposed that resident and migratory birds do not compete in montane habitats (O'Donnell et al. 2014), it should be assessed in lowland habitats and preferably, across an elevation gradient. Incorporating the natural history, the type of interaction (i.e., predation, mutualism, commensalism; Fig. 1), and the gradient of interaction intensity at different spatial and temporal scales will improve our understanding of the biogeography of interactions and disentangle the patterns of range overlap in cases of predation, mutualism, and commensalism.

Conclusion

In summary, our work assesses the intensity of interaction as determinant of geographic range overlap between ant-following birds and army ants. Bayesian regression models found no support for higher range overlap between obligate

ant-following birds and army ants, compared to facultative ant-following birds, or for wider geographic ranges in facultative ant-following birds, compared to obligate ant-following birds. However, our analyses show a trend, for both, higher percentages of range overlap between obligate ant-following birds and army ants, and higher geographic ranges of facultative ant-following birds extending to areas with no army ants. Understanding the biogeography of biotic interactions, especially parasitism interactions, requires knowledge of the natural history of the species, integrated here through the comparison of species with obligate ant-following behavior and species with facultative behavior. Our results suggest that the approach to a predictive biogeography of interactions will require that biotic interactions be studied as part of a quantitative gradient of intensities and not as qualitative categories, and that spatial and temporal variation in the intensity of interaction be integrated in models to allow for inferences to be made from the local scale to the regional scale.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Ana Lucía Interiano: conceptualization, data curation (equal), formal analysis, investigation, methodology (lead), visualization, writing – original draft, writing – review and editing. Dulce Herrera: conceptualization, data curation (equal), formal analysis, investigation, methodology, visualization, writing – original draft, writing – review and editing. Habibi Orellana Carrera: conceptualization, data curation (equal), formal analysis, investigation, methodology, visualization, writing – original draft, writing – review and editing. Nery D. Monroy R.: conceptualization, investigation, visualization, writing – review and editing. Pavel García: formal analysis (lead), methodology, visualization, writing – original draft, writing – review and editing. Jorge Erwin López: conceptualization, supervision, writing – review and editing. Rosa Alicia Jiménez: conceptualization (lead), formal analysis, investigation, methodology, project administration, supervision, validation, visualization, writing – original draft (lead), writing – review and editing.

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Data availability

Global Biodiversity Information Facility downloads citations and records from The Macaulay Library are included in the main document. R code available at <https://github.com/pavka17/Ant-following-bird-project>.

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Supplementary material 1

Supplementary information

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Data type: docx

Explanation note: **table S1**. Final sets of bioclimatic variables used to build the Species Distribution Models for each species of army ants and ant-following birds. **table S2**. Area under the curve (AUC) and threshold values for each species of army ants and ant-following birds.

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